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MICROZOOPLANKTON GRAZING AND PRODUCTIVITY IN THE CENTRAL AND SOUTHERN SECTOR OF THE INDIAN RIVER LAGOON, FLORIDA

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ABSTRACT: Microzooplankton grazing was measured with the dilution method in the central and southern sectors of the Indian River Lagoon during summer 2006 and 2007. Microzooplankton actively grazed phytoplankton during all experiments. Grazing rates averaged (\pm SD) 0.95 \pm 0.19 d⁻¹ and ranged from 0.54 to 1.36 d⁻¹. Phytoplankton carbon, measured by microscopy, averaged 314 \pm 251 µg C L⁻¹ and ranged from 115 to 936 µg C L⁻¹. Microzooplankton ingestion rates averaged 303 \pm 260 µg C L⁻¹d⁻¹ and ranged from 90 to 907 µg C L⁻¹d⁻¹. Microzooplankton potential productivity, a first-order estimate of microzooplankton productivity, averaged 91 \pm 78 µg C L⁻¹d⁻¹ and ranged from 27 to 272 µg C L⁻¹d⁻¹. Microzooplankton grazing rates were not related to salinity. In contrast, the magnitudes of phytoplankton carbon concentration, microzooplankton ingestion rate, and microzooplankton potential productivity were statistically significantly greater in lower (<20 psu) salinity waters. An examination of data from another Florida estuary and other Gulf of Mexico coast estuaries suggests that microzooplankton productivity may, in general, be highest in lower salinity waters.

Key Words: estuary, phytoplankton, microzooplankton, salinity, fish larvae, critical habitat

A large portion of the commercial and recreational fish in the United States use Florida estuaries as nurseries. Many fish species that use estuaries as nurseries have planktotrophic larvae that primarily feed on zooplankton. While mesozooplankton are important prey for late larval stages, micro-zooplankton are important prey for young larvae (Govoni et al., 1983; Stoecker and Govoni, 1984). The availability of microzooplankton is considered critical to the survival of first-feeding larvae and later year class strength (Helfman et al., 1997 and references therein). Microzooplankton, in practice typically defined as zooplankton $<202 \,\mu m$ in size, consist of a diverse assemblage of protists and metazoans of different sizes and nutritional values. Copepod nauplii and copepodites within the microzooplankton community are generally considered to be the main prey of young larvae. However, they can be too large and mobile for first-feeding larval fishes to feed upon (Stoecker and

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Govoni, 1984; Stoecker and Capuzzo, 1990; Nagano et al., 2000). Young larvae can feed on other constituents of the microzooplankton community, such as ciliates and dinoflagellates (Govoni et al., 1983; Stoecker and Govoni, 1984). Ciliates and dinoflagellates are an abundant constituent of the microzooplankton community in many estuaries (Buskey, 1993 and references therein) and, due to their size; mobility, and biochemical composition, can be a high quality prey for first-feeding larvae (Stoecker and Capuzzo, 1990; Nagano et al., 2000).

Since is not feasible to protect and manage entire estuaries, fisheries management requires that the critical habitats within estuaries be identified and protected (Beck et al., 2001; Levin and Stunz, 2005). Microzooplankton are considered important to the growth and survival of many first-feeding planktotrophic larvae. Therefore, neritic estuarine habitat where the highest magnitude of microzooplankton productivity occurs might be critical estuarine habitat.

At present, there is no method to directly estimate the productivity of the microzooplankton community. A first-order estimate of microzooplankton productivity, hereafter referred to as microzooplankton potential productivity, can be calculated with rate estimates of microzooplankton ingestion on phytoplankton and assuming that gross growth efficiency is constant (Landry and Calbet, 2004). Microzooplankton potential productivity calculated with this approach was found to be greatest in the lower (<20 psu) salinity waters of Apalachicola Bay, a relatively pristine Florida gulf coast estuary (Putland and Iverson, 2007a). Another study in Apalachicola Bay (Putland and Iverson, 2007b) indicated that the rate at which copepod nauplii are produced is highest in lower (<20 psu) salinity waters. To determine if this trend for microzooplankton productivity in Apalachicola Bay is representative of Florida estuaries, it is necessary to conduct similar studies of microzooplankton across the salinity gradient in other Florida estuaries. In the present study, microzooplankton potential productivity was estimated in Indian River Lagoon, a Florida Atlantic coast estuary. Indian River Lagoon is considered one of the most biological diverse estuaries in North America and has been subjected to increasing freshwater, nutrient, and pollution input (Sigua and Tweedale, 2003; Lin et al. 2008; Schuler and Rand 2008). Our results suggest that the trend between microzooplankton potential productivity and salinity in Indian River Lagoon is similar to that observed in Apalachicola Bay.

MATERIALS AND METHODS—*Physical environment*—Seawater was collected from Indian River Lagoon (Florida Atlantic Coast, USA), a restricted subtropical lagoon (Fig. 1). Indian River Lagoon is a shallow (average depth is 2 to 3 m) and generally well mixed estuary. Salinity in the lagoon ranges from 15 to 35 psu, with lowest salinity typically in the northern sector of the lagoon. Exchange between the lagoon and Atlantic shelf waters occurs via three openings (Sebastian Inlet, Fort Pierce Inlet, St. Lucie Inlet) through the barrier islands. The 50% renewal time ranges from days in the southern sector to a year in the northern sector of the lagoon (Smith, 1993). The minimum seawater temperature is about 10°C during winter and maximum temperature is about 31°C during summer.



FIG. 1. The sampling stations in Indian River Lagoon (Florida Atlantic Coast, USA). The stations refer to the locations where water was collected for microzooplankton grazing experiments.

PUTLAND AND SUTTON—MICROZOOPLANKTON GRAZING No. 3/4 2010] IN INDIAN RIVER LAGOON

TABLE 1. Phytoplankton growth rate (μ , d⁻¹), microzooplankton grazing rate on phytoplankton (g, d⁻¹), coefficient of determination (r²) for linear dilution plots, in situ chlorophyll (Chl a, μ g L⁻¹), in situ total phytoplankton carbon (PC, μ g C L⁻¹), microzooplankton ingestion rate on phytoplankton (I_c, μ g C L⁻¹d⁻¹) at various surface temperatures (°C) and salinities (psu) in Indian River Lagoon, Florida Atlantic Coast, USA. All regressions were significant at p < 0.05.

Date	Station	Temp.	Salinity	μ	g	r ²	Chl a	PC	I_c
09 Aug 06	1	27.3	29.4	0.64	0.91	0.39	1.8	114.6	91.4
09 Aug 06	2	30.8	33.2	0.64	0.91	0.39	2.7	199.8	159.4
09 Aug 06	3	30.5	34.0	0.64	0.91	0.39	2.0	172.9	138.0
15 Aug 06	4	30.6	33.1	-0.12	0.75	0.56	8.2	286.7	143.6
15 Aug 06	5	30.6	35.8	1.47	0.88	0.96	1.5	126.9	152.3
15 Aug 06	6	30.8	35.9	0.58	0.77	0.85	2.8	132.5	93.0
28 Sep 06	7	27.0	23.6	1.65	1.36	0.95	3.4	218.5	344.9
28 Sep 06	8	28.0	5.0	2.13	1.13	0.98	4.0	128.6	250.0
28 Sep 06	9	28.0	31.1	0.77	1.15	0.94	2.8	152.0	145.5
18 Oct 06	10	27.4	15.9	1.00	0.94	0.95	12.6	936.0	907.3
18 Oct 06	11	26.9	20.1	1.23	0.92	0.96	4.7	796.1	859.3
18 Oct 06	12	26.1	34.3	0.69	0.97	0.92	4.1	474.0	401.2
25 Apr 07	13	24.2	23.8	1.12	0.91	0.95	2.1	430.0	435.8
25 Apr 07	14	24.1	28.7	0.89	1.20	0.94	4.1	319.0	329.2
25 Apr 07	15	24.0	38.3	0.24	0.54	0.82	2.0	219.0	102.2

Sampling—Seawater was sampled from 15 stations during summer 2006 and 2007 from the central and southern sector of the Indian River Lagoon (Fig. 1, Table 1). Seawater was collected between surface and 0.5 m depth with a 20-L darkened polycarbonate carboy.

Irradiance was measured at the surface and depth of collection with a model 192SA Li-Cor underwater quanta sensor attached to a handheld meter. The collected seawater was measured for temperature and salinity with an YSI salinometer and sub-sampled for phytoplankton analyses. Samples (500 mL) for the analysis of chlorophyll were stored on ice in polyethylene bottles for <4 hr prior to being filtered. Samples (20 mL) for the analysis of phytoplankton <20 µm in size were preserved with glutaraldehyde (2% final concentration) and stored in darkness at 4°C (MacIsaac and Stockner, 1993). Samples (125 mL) for the analysis of eukaryotic phytoplankton >20 µm in size were preserved with acid Lugol's (2% final concentration) and stored in darkness at 4°C. The remainder of the collected seawater was reserved for microzooplankton grazing experiments.

Sample analysis and processing - Chlorophyll concentration—Samples for the analysis of chlorophyll were filtered through 47-mm GF/F filters at <117 mm Hg vacuum. Filtered samples were stored in darkness at -20° C and analyzed within one week of sample collection. Chlorophyll a was extracted from filters in 90% acetone for 24 hr at -20° C. The concentration of chlorophyll a was measured fluorometrically with a Model 10 Turner Designs fluorometer equipped with filter sets for optimal sensitivity of chlorophyll a in the presence of chlorophyll b (Welschmeyer, 1994).

Phytoplankton abundance—Samples for the analysis of phytoplankton $<20 \ \mu\text{m}$ in size were enumerated within 1 week of sample collection. Samples (10 to 20 mL) were filtered ($<117 \ \text{mm}$ Hg vacuum) onto 0.4- μ m black Poretics polycarbonate filters and then the filters were mounted with Cargille type B immersion oil onto glass slides. Cyanobacteria picophytoplankton were visualized at a total magnification of $\times 1250$ with a BH2 Olympus epifluorescence microscope equipped with a green excitation filter set (excitation: 480 to 550 nm; emission: 590 to 700 nm) (MacIsaac and Stockner, 1993). Phycoerythrin- and phycocyanin- containing cyanobacteria were identified as

orange and red, respectively fluorescing coccoid cells with a diameter of between 1 to 2 μ m. Eukaryotic phytoplankton <20 μ m in size were visualized at a total magnification of ×1250 with a BH2 Olympus epifluorescence microscope equipped with a custom filter set (500DCXR C88453) having excitation and emission spectra between 400 to 480 nm and 520 to 700 nm, respectively (MacIsaac and Stockner, 1993). Eukaryotic phytoplankton were identified as red fluorescing cells. For each sample, at least 100 cells for each phytoplankton group (eukaryotic phytoplankton <20 μ m in size, phycoerythrin containing cyanobacteria, and phycocyanin containing cyanobacteria) were counted (Hobro and Willén, 1977). Cells were counted from filters in either transects or in a minimum of ten random fields.

Samples for the analysis of eukaryotic phytoplankton >20 μ m in size were enumerated within one month of sample collection. Samples (10 to 50 mL) were settled for 24 hr with Utermöhl settling chambers. Cells were viewed at a total magnification of ×200, through phase contrast light microscopy, with a CK2 Olympus inverted microscope. Cells were identified to the lowest possible classification (i.e. species or genera or group) following Tomas (1997). For each settled sample, at least 100 cells of the most abundant phytoplankton category were counted (Hobro and Willén, 1977). Cells were counted from the settled samples in transects.

Phytoplankton carbon—Phytoplankton carbon concentration was calculated with cell carbon: cell volume formulae and estimates of phytoplankton abundance and cell volume. Carbon to volume formulae for diatoms and other protists were used (Menden-Deuer and Lessard, 2000). Twenty measurements of cell dimensions were taken for each abundant phytoplankton category per sample. Cell volumes were estimated with simple geometric volume formulae (Wetzel and Likens, 1991). Cell volumes were corrected for shrinkage caused by fixation. For autotrophs <20 µm in size, except cyanobacteria, cell volume was multiplied by 1.52 (Booth et al., 1993). The cell volume for autotrophs that were preserved in Lugol's was multiplied by 1.33 (Montagnes et al., 1994). The *in situ* total phytoplankton carbon concentration (PC, µg C L⁻¹) was estimated as the sum of carbon from cyanobacteria picophytoplankton and eukaryotic phytoplankton.

Microzooplankton grazing assays—The dilution technique (Landry and Hassett, 1982) was used to estimate the rates of phytoplankton growth and microzooplankton grazing on phytoplankton. Prior to conducting microzooplankton grazing experiments, all equipment that would contact seawater was acid washed with 10% hydrochloric acid. Afterward, equipment was thoroughly rinsed and then soaked for several days with Nanopure water. Nitrile gloves were worn during all water handling procedures.

Diluent was prepared by filtering seawater through 0.2-µm Pall-Gelman capsule filters. The target dilutions (seven dilutions, one bottle per dilution) per dilution assay were 95, 85, 75, 65, 55, 45, 35, and 0% diluent. Appropriate volumes of diluent were added to 2-L polycarbonate incubation bottles. The <202-µm seawater fraction was then added to bottles by dispensing seawater through silicon tubing that was equipped with 202-µm Nitex screen. The silicon tubing was kept submerged below the waterline in the bottles to reduce damage to microzooplankton. Nitrogen (as ammonium chloride) was added to the incubation bottles because it is the nutrient that most frequently limits phytoplankton productivity throughout Indian River Lagoon (Phlips et al., 2002). Approximately 10 μ g N L⁻¹ was added to each dilution bottle. For each dilution assay conducted, two additional 0% diluent bottles did not receive the nutrient enrichment and therefore served as controls to estimate the non-nutrient enriched rates of phytoplankton growth. Chlorophyll was sampled (duplicate 250 mL samples per bottle) from all bottles immediately after preparing the dilution treatments and again after 24 hr. Chlorophyll samples were stored and analyzed following the procedures previously mentioned. Incubation bottles were placed inside bags of neutral density screen to simulate the light energy from the collection site. The bottles were incubated in situ in the Indian River Lagoon channel at Harbor Branch Oceanographic Institution.

Rates of phytoplankton growth and microzooplankton grazing—The rates of phytoplankton growth and microzooplankton grazing on phytoplankton were estimated with Model I linear

regressions of phytoplankton apparent growth rate (AGR) versus actual dilution factor (ADF) (Landry and Hassett 1982). The ADF for each bottle was calculated as:

$$ADF = [T_o chl a(X_i)] \times [T_o chl a(X_o)]^{-1},$$
(1)

where T_o chl a (X_i) is the time zero chlorophyll a concentration at target dilution factor X_i and T_o chl a (X_o) is the time zero chlorophyll a concentration of the 0% diluent treatment. The phytoplankton AGR (d⁻¹) in each incubation bottle was calculated as:

$$AGR = [t^{-1}] \times [ln(P_t \times P_o^{-1})], \qquad (2)$$

where t is the duration of the incubation (1 day) and P_o and P_t refer to initial and final chlorophyll concentration, respectively. The y-intercept of the linear regression is the nutrient enriched rate of phytoplankton growth in the absence of grazing. The absolute value of the negative slope is the rate of microzooplankton grazing (g, d⁻¹), equivalent to the microzooplankton community clearance rate (mL cleared indiv.⁻¹ d⁻¹ × indiv. mL⁻¹). Rates of non-nutrient enriched phytoplankton growth (μ , d⁻¹) were calculated as the sum of the average apparent growth rate calculated from the control bottles (AGR_{control}, d⁻¹) and the rate of microzooplankton grazing (g, d⁻¹).

Microzooplankton ingestion rate on phytoplankton (I_c, $\mu g \ C \ L^{-1} \ d^{-1}$) was calculated as:

$$I_{c} = g \times C_{m}, \tag{3}$$

where C_m is the mean phytoplankton carbon concentration (µg C L⁻¹) during the grazing experiment calculated as:

$$C_{m} = \left[PC \left(e^{(\mu - g)t} - 1 \right) \right] \times [(\mu - g)t]^{-1}, \tag{4}$$

where t is 1 day and PC is the in situ total phytoplankton carbon concentration ($\mu g \ C \ L^{-1}$) determined from samples collected in the field.

Microzooplankton potential productivity (MPP, $\mu g C L^{-1} d^{-1}$) was calculated as:

$$MPP = I_c \times Gross \ Growth \ Efficiency.$$
(5)

Gross Growth Efficiency was assumed to be 30% (Landry and Calbet, 2004).

Statistical analyses—Two-sample t tests were used to determine if parameters were significantly different among lower (< 20 psu) and higher (>20 psu) salinity estuarine waters. Data sets were tested for normality (with the Kolmogorov-Smirnov test) and equality of variances (with the Levene's test). In cases where assumptions of normality and/or equal variance were not met, Mann-Whitney non-parametric tests were performed. For all statistical analyses, a p-value of less than 5% was used to determine significance (Sokal and Rohlf, 1995).

RESULTS—Microzooplankton actively grazed phytoplankton during all experiments. Grazing rates averaged (\pm SD) 0.95 \pm 0.19 d⁻¹ and ranged from 0.54 to 1.36 d⁻¹. Phytoplankton carbon averaged 314 \pm 251 µg C L⁻¹ and ranged from 115 to 936 µg C L⁻¹. Microzooplankton ingestion rates averaged 303 \pm 260 µg C L⁻¹d⁻¹ and ranged from 90 to 907 µg C L⁻¹d⁻¹ (Table 1). Microzooplankton grazing rates were not statistically significantly greater in lower (<20 psu) salinity waters. In contrast, phytoplankton carbon concentration and microzooplankton ingestion rate were statistically significantly

TABLE 2. Average (± S.D.) values for variables during summer in lower and higher salinity waters of Indian River Lagoon. Averages were estimated from all available data collected within each salinity range. Variables include total phytoplankton carbon (PC, $\mu g \ C \ L^{-1}$), microzooplankton grazing rate on phytoplankton (g, d⁻¹), microzooplankton ingestion rate on phytoplankton (I_c, $\mu g \ C \ L^{-1} \ d^{-1}$), and microzooplankton potential productivity (MPP, $\mu g \ C \ L^{-1} \ d^{-1}$). Results of two-sample t and Mann-Whitney tests, testing for differences between lower and higher salinity waters, are denoted as * for p < 0.05 and ns for not significant (p > 0.05).

Variable	Lower (<20 psu) Salinity n=3	Higher (>20 psu) Salinity n=12	Significance
PC	620 (431)	237 (118)	*a
g	1.0 (0.1)	0.9 (0.2)	ns
I _c	672 (366)	211 (128)	*a
MPP	202 (110)	63 (38)	*a

^a Mann-Whitney test

greater in lower salinity waters (Table 2). Microzooplankton potential productivity, a first-order estimate of microzooplankton productivity, averaged 91 \pm 78 µg C L⁻¹d⁻¹ and ranged from 27 to 272 µg C L⁻¹d⁻¹. Microzooplankton potential productivity was statistically significantly greater in lower salinity waters (Table 2; Fig. 2).

DISCUSSION—Methodological considerations—In the present study phytoplankton carbon concentration was estimated in order to calculate microzooplankton potential productivity. Phytoplankton carbon concentration can be estimated with estimates of chlorophyll concentration and by applying assumed carbon: chlorophyll ratios. Alternatively, phytoplankton carbon concentration can be estimated through microscopy. In the former method, the estimate of phytoplankton carbon concentration has error associated with the measurement of chlorophyll and the use of assumed phytoplankton carbon: chlorophyll ratios (Kruskopf and Flynn, 2006). Microscopic estimates of phytoplankton carbon concentration also have measurement error, but also have error associated with cell carbon: cell volume formulae (Menden-Deuer and Lessard, 2000), estimates of cell volume (Wetzel and Likens, 1991), estimates of cell abundance (Hobro and Willén, 1977), and corrections to cell volume caused by fixation (Booth et al., 1993; Montagnes et al., 1994). Additional error in microscopic estimates of phytoplankton carbon concentration may exist if some phytoplankton taxa have, for example, unique cell carbon: cell volume formulae, cell volumes, or responses to fixatives at different salinities.

The rates of phytoplankton growth and microzooplankton grazing were determined with the dilution method of Landry and Hassett (1982). The dilution method assumes that phytoplankton growth is exponential and constant across the dilution gradient, that micrograzers are not food-satiated, and that grazing varies with the density of micrograzers. Several factors can lead to violation of these assumptions and therefore erroneous estimates of phytoplankton growth rate and microzooplankton grazing rate. For example, differences in nutrient



FIG. 2. Microzooplankton potential productivity during summer in Indian River Lagoon, Florida Atlantic Coast (filled symbols, present study); Oyster Bayou, Texas gulf coast (open symbols, Dagg 1995); and Apalachicola Bay, Florida gulf coast (line, Putland and Iverson 2007a).

concentration across the dilution gradient can lead to differences in phytoplankton growth rate across the dilution gradient. In Indian River Lagoon, nitrogen is the nutrient that most frequently limits phytoplankton (Phlips et al., 2002). Therefore, in the present study, nitrogen was added to all the incubation bottles to prevent nitrogen limitation. Although phytoplankton growth rates could have been limited by phosphorus, the observation that none of the dilution plots had positive slopes suggests that phytoplankton growth rates were not phosphorus limited, or differed substantially, across the dilution gradient.

Differences in the light level among the incubation bottles of the dilution experiments is another factor that can lead to differences in phytoplankton growth rate across the dilution gradient. This is typically a problem for dilution experiments conducted with water from turbid estuaries: incubation bottles with the most diluent tend to have the least amount of color, or most amount of light (Murrell and Hollibaugh, 1998). Phytoplankton growth rates can be highest in bottles with the most diluent and, as a result, growth rates can be overestimated. Alternatively, phytoplankton in bottles with the most diluent may photoadapt. A reduction of cellular chlorophyll content in phytoplankton in bottles with the most diluent can lead to an underestimation of phytoplankton growth rates. In the present study, there were no observed differences in color among the bottles to suggest that phytoplankton growth rates were unequal across the dilution gradient. FLORIDA SCIENTIST

It is unlikely that microzooplankton were food-satiated during our experiments. Non-linear dilution plots, indicative of feeding thresholds or saturated feeding (Gifford, 1988; Gallegos, 1989; Dolan et al., 2000; Moigis, 2006) were not observed in the present study. All dilution plots were linear, with an average (\pm S.D.) coefficient of determination of 0.83 (\pm 0.18), suggesting that microzooplankton were not satiated (Table 1). Microzooplankton grazing rates, however, might have been affected by micrograzer growth. Like most microzooplankton grazing studies, in the present study grazing rates were not corrected for micrograzer growth. If there was substantial microzooplankton growth, then microzooplankton grazing rates might have been overestimated (Gallegos, 1989, Dolan et al., 2000).

Microzooplankton productivity-Microzooplankton potential productivity is a first-order estimate of microzooplankton productivity and can be calculated with rate estimates of microzooplankton ingestion on phytoplankton and assuming that gross growth efficiency is constant (Landry and Calbet, 2004). With this method we calculated microzooplankton potential productivity in Indian River Lagoon. Based on the statistical tests performed, microzooplankton potential productivity was significantly greater in lower (<20 psu) salinity waters of Indian River Lagoon (Table 2). However, due to the small sample sizes, particularly in lower (<20 psu) salinity waters, these results should be interpreted with caution. Microzooplankton potential productivity in Indian River Lagoon, and possibly Oyster Bayou, a Louisiana gulf coast estuary, appears to be related to salinity in a fashion similar to that observed in Apalachicola Bay (Fig. 2). A similar relationship may occur in other estuaries. Although the study (Jochem, 2003) did not examine microzooplankton ingestion of the entire phytoplankton community, microzooplankton ingestion of heterotrophic bacteria and phototrophic pico- and nanoplankton peaked in lower salinity waters of the Mississippi River plume. In East Lagoon, a Texas gulf coast estuary, the rate at which copepod nauplii (a component of microzooplankton, see Introduction) are produced is also highest in lower (<20 psu) salinity waters (Ambler, 1985). While additional data would be useful to confirm the relationship, the observation that microzooplankton potential productivity peaks in the lower salinity waters among the estuaries examined suggests that this is a general trend among Florida estuaries and estuaries bordering the Gulf of Mexico.

Microzooplankton are important prey for many larval fishes (Stoecker and Govoni, 1984; Stoecker and Capuzzo, 1990). The results from this study suggest that larval fishes may access a higher quantity of microzooplankton productivity in lower (<20 psu) salinity estuarine waters. If future field studies discover that higher quantities of microzooplankton productivity improve first-feeding larval survival and later year class strength (Helfman et al., 1997 and references therein), then the lower salinity waters of Florida estuaries, and possibly other gulf coast estuaries, could be considered critical estuarine nursery habitat.

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